

A new sessile barnacle (Cirripedia, Brachylepadoromorpha) from the Lau Back-Arc Basin, Tonga; first record of a living representative since the Miocene

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Abstract. — An extant representative of the Brachylepadoromorpha, *Neobrachylepas relicha* gen. et sp. nov., has been discovered associated with hydrothermal vents in the Lau Basin. The suborder, comprising the earliest sessile barnacles, appeared in the Jurassic. It underwent a modest diversification before the close of the Cretaceous, when it began to decline concomitant with the origin and diversification of the modern sessile barnacles (Verrucomorpha and Balanomorpha) as well as certain shell-crushing predators, and it has been absent from the fossil record since the Miocene. Thus *Neobrachylepas* is unique among previously known hydrothermal vent barnacles, *Neolepas* (Scalpellomorpha), *Neoverruca* (Verrucomorpha) and *Eochionelasmus* (Balanomorpha), in being the only known living member rather than simply the most primitive living member of its respective suborder. The Lau Basin fauna includes representatives of all four of these suborders and therefore represents the most diverse cirriped fauna of any known hydrothermal vent community.

Keywords. — Mesozoic relics, hydrothermal vents, center of diversity.

Un nouveau cirripède sessile (Cirripedia, Brachylepadoromorpha) de l'arc postérieur du bassin de Lau, Tonga; première observation d'un représentant vivant de ce groupe non signalé depuis le Miocène

Résumé. — Un représentant actuel des Brachylepadoromorpha, *Neobrachylepas relicha*, n. gen., n. sp., a été découvert dans les sources hydrothermales du bassin de Lau. Le sous-ordre, comprenant les cirripèdes les plus anciens, est apparu au Jurassique. Il subit ensuite une diversification modeste avant la fin du Crétacé, à partir duquel il commença à décliner en même temps qu'apparaisaient et se diversifiaient les cirripèdes modernes (Verrucomorpha et Balanomorpha), tout comme certains prédateurs broyeurs de coquilles ; il était absent depuis cette mention fossile du Miocène. Ainsi, *Neobrachylepas* est unique parmi les cirripèdes déjà connus de sources hydrothermales : *Neolepas* (Scalpellomorpha), *Neoverruca* (Verrucomorpha) et *Eochionelasmus* (Balanomorpha), en étant le seul membre vivant connu plutôt que simplement le plus primitif de ce sous-ordre. La faune du bassin de Lau inclut des représentants des quatre sous-ordres et représente ainsi la faune de cirripèdes la plus diversifiée de toutes les communautés connues de sources hydrothermales.

Mots-clés. — Reliques du Mésozoïque, sources hydrothermales, centre de diversité.

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INTRODUCTION

Explorations of deep-sea hydrothermal vents, beginning a little more than 15 years ago, have revealed a remarkable diversity of unusual invertebrates many of which are endemic at relatively high taxonomic levels (MCLEAN, 1985; NEWMAN, 1985; TUNNICLIFFE, 1991). Some

of the animals encountered were evidently derived from taxa found in the surrounding deep sea, or from those inhabiting “cognate” environments such as cold and hydrocarbon seeps (NEWMAN, 1985), dead whales (SMITH *et al.*, 1989), and sunken wood (DANDO *et al.*, 1992). But many currently have no known living representatives from which they could have been derived, and this is particularly true among the barnacles (YAMAGUCHI & NEWMAN, 1990). This raises questions regarding not only the origin but the age of the present hydrothermal vent fauna. Furthermore, the new barnacle to be described herein, from the Lau Back-Arc Basin, Tonga (NAUTILAU, 1991), belongs to the Brachylepadorpha, the most primitive suborder of sessile barnacles which appeared in the fossil record in the Jurassic only to disappear in the Miocene. Therefore knowledge of the new form is relevant to understanding the early phylogeny of the sessile barnacles as well as the origin and age of vent faunas, and these subjects will also be taken up following the systematic account.

In addition to contributing to our understanding of the diversity and origin of the vent fauna and sessile barnacles, the discovery of a living brachylepadorph is exciting for a morphologist because it makes possible studies of its soft parts and internal organs. It is also of importance to ecologists because it permits study of life history strategies including planktonic larval and benthic stages. It will be important to sort out those properties that are basic to the group from those that have been developed as adaptations to the hydrothermal vent habitat. The obligate association of *Neobrachylepas*, as well as other primitive barnacles such as *Neolepas*, *Neoverruca* and *Eochionelasmus*, makes it inescapable that the association with the hydrothermal environment has persisted for an extensive period of time.

SYSTEMATICS

Subclass CIRRIPEDIA Burmeister, 1834 (= Cirrhipèdes Lamarck, 1806 : Cambrian-Recent)

Superorder THORACICA Darwin, 1854 (Cambrian-Recent)

Order SESSILIA Lamarck, 1818 (Upper Jurassic-Recent)

Suborder BRACHYLEPADOMORPHA Withers, 1923 (Upper Jurassic-Recent)

Family BRACHYLEPADIDAE Woodward, 1901 (Upper Jurassic-Recent)

DIFFERENTIAL DIAGNOSIS (emend.)

Symmetrical sessile barnacles having an operculum generally including a pair of latera as well as paired scuta and terga (scuta and terga alone in Balanomorpha), a primary wall consisting of but two plates, rostrum and carina (plus at least two pairs of dedicated latera in Balanomorpha), and a secondary wall of imbricating plates occurring in whorls of as many as eight in which case the uniform vertical tiers stand four plates high (whorls not arranged in uniform tiers in Balanomorpha). The whorls are added successively during ontogeny, inside the previous whorl (outside the previous whorl in Balanomorpha), and the basal margins of plates of the first few whorls are usually equipped with interlocking devices (not found in Balanomorpha).

NEOBRACHYLEPAS gen. nov.

TYPE. — *Neobrachylepas relicca* sp. nov.

ETYMOLOGY. — From the Greek *neo* (new), *brachy* (short), and *lepas* (shellfish); and *relicca*, from the French *relique*, last survivor of an ancient radiation, in contrast to *relicte*, a population separated from its parent population (French Biogeographical Society, 1947 according to UDVARDY, 1969).

DIAGNOSIS

A brachylepadomorph with the operculum superficially resembling that of balanomorphs but differing in the terga and scuta not being distinctly articulated, in retaining the median latera, and in having depressor muscles more or less evenly distributed rather than concentrated in discrete bundles along the basal margin of the scutum and tergum. The whorls of imbricating plates agree with those of some other brachylepadomorphs in standing in tiers three rather than four plates high, but the plates of the basal whorls differ from those of all known brachylepadomorphs in lacking basal interlocking or ligamentous devices.

Furthermore, the form of the shell is 1), low (peltate) rather than high and 2), the carina and rostrum abut at their lateral margins (as they do on the movable side of *Neoverruca*) rather than there being a gap between them protected by imbricating plates as is apparently the case in other brachylepadomorphs, or filled by two or three pairs of dedicated latera as in balanomorphs. The basis is membranous. The trophi, and the cirri except for details of the first two pairs, are similar to those of other hydrothermal vent barnacles.

Neobrachylepas relicca sp. nov.

(Figs 1-5)

MATERIAL. — Knowledge of the new form, the first living brachylepadomorph ever examined, is based on seven specimens, some of which are minute and many if not all of which are juveniles (may not have completed shell development; see measurements below). The largest (7.6 mm in rostro-carinal diameter) was almost completely buried under a friable coating of sulfide and oxide deposits, as was a juvenile of *Eochionelasmus ohtai* of a comparable size a few centimeters from it (Fig. 1). The former, designated the holotype (see below), has been left intact. The other specimens either had been or were removed from the substratum. These were variously dissected, including the second largest which has been designated the first paratype (Fig. 2).

The seven type specimens, ranked according to size (length = R-C diameter, in mm) in the following table, have been deposited in the following museums: MNHN = National Museum of Natural History, Paris; NSMT = National Science Museum, Tokyo; USNM = United States National Museum of Natural History, Washington, DC. Length [L] is the rostro-carinal diameter and width [W] is the lateral diameter, in mm):

Sample	L	W	Type designation	Depository
1. BL04	7.6	5.7	holotype	MNHN-Ci 2290
2. BL01	6.5	6.0	1st paratype	USNM-274137
3. BL04	3.2	2.1	3rd paratype	MNHN-Ci 2386
4. BL03	2.5	1.7	2nd paratype	NSMT-Cr 14111
5. BL04	1.7	1.0	4th paratype	MNHN-Ci 2387
6. BL12	1.3	0.6	5th paratype	MNHN-Ci 2388
7. BL04	≈ 0.1		6th paratype	MNHN-Ci 2389

This material, received from the Centre national de tri d'océanographie biologique (CENTOB), Brest, was collected from two stations by the French submersible *Nautille* during the Biolau cruise (May 1989) to the Lau Basin, SW Pacific.

Station 1. "Hine Hina" (station without smokers), 22°32'S, 176°43'W; sample BL01, 1842 m, and BL03, 1870 m, the latter about 750 m south of Hine Hina.

Station 2. "Vailili" (station with smokers), 22°13'S, 176°38'W; samples BL04, 1739 m and BL12, 1730 m.

HABITAT. — The general nature of the vent communities at Lau have been elucidated by DESBRUYÈRES *et al.* (1994). A general account of metallogenesis in the basin is given by FOUQUET *et al.* (1991) and the following description of this habitat was provided by D. JOLLIVET (pers. comm.). It consisted of a depression formed by a large fissure surrounded by mounds of very porous fragments of basalt having a whitish cast due to alteration. Low temperature waters (2-19° C) were percolating through a large mussel bed inhabited by crabs and fishes and surrounded by clumps of barnacles on escarpments and large basaltic boulders subject to the deposition of sulfides and oxides.

The barnacles dominated the outer rim of most sites and are analogs of the filter-feeding serpulids of East Pacific Rise sites (DESBRUYÈRES *et al.*, 1994). Those observed at Lau included a *Neolepas*-like form and *Eochionelasmus ohtai*, the latter being physically closest to the mussels. The first specimen of *Neobrachylepas relicha* to come to our attention was sample BL 01. In addition to *Neobrachylepas*, a single specimen of a unique and apparently mature neoverrucid was encountered in the material collected. Thus Lau, in having representatives of four suborders of the thoracican cirripeds (Scalpellomorpha, Brachylepadomorpha, Verrucomorpha, and Balanomorpha) not only includes the most unusual but the most diverse hydrothermal vent barnacle fauna known.

Considering the generally gregarious nature of vent barnacles taken elsewhere, as well as in the Lau Basin, and that *Neobrachylepas relicha* is a functional hermaphrodite, it is likely that the infrequently encountered and mostly juvenile specimens of this species were waifs from preferred microhabitats rather than representatives of a sparsely distributed population. If the species were large as well as gregarious, as are *Neolepas*, *Neoverruca* and *Eochionelasmus*, it would have been conspicuous and therefore more likely collected. But if a small species, as it seems to be, with a shell that is readily masked by sulfide and oxide deposits, it would be hard to detect in the field even if gregarious, and small size can also provide a refuge from predation from fish, neogastropods and the like.

DIAGNOSIS

As for the genus. The soft parts of other brachylepadomorphs are unknown but, as expected, the present species is hermaphroditic. While its cirri are similar to those of all previously known hydrothermal vent barnacles (suborders Scalpellomorpha, Verrucomorpha and Balanomorpha), cirrus II is unusual in being relatively short and non-antenniform. The species differs from all thoracican cirripeds in having a median dorsal appendage on the prosoma that apparently holds an egg mass in place when brooding.

COMPARATIVE DESCRIPTION

Hard parts

The low-conic profile of *Neobrachylepas relicha* is accentuated by the apexes of the opercular valves being tipped back towards the carina in a stance more characteristic of balanomorphs than any previously known brachylepadomorphs. Indeed, *N. relicha* is, in general appearance, remarkably similar to the balanomorph *Eochionelasmus ohtai* whose distribution, at Lau, it overlaps (Fig. 1). But as can be seen, even in this figure, the similarity is cursory; *e.g.*, the operculum of *Neobrachylepas* (Figs 1, 2, 3) includes a pair of small latera as well as the paired scuta and terga, and its wall lacks the two pairs of dedicated latera seen in the *Eochionelasmus*.

The operculum is capable of movements independent of the wall, as it is in balanomorphs but not scalpellomorphs (DARWIN, 1852), even though the details of its plates and the associated

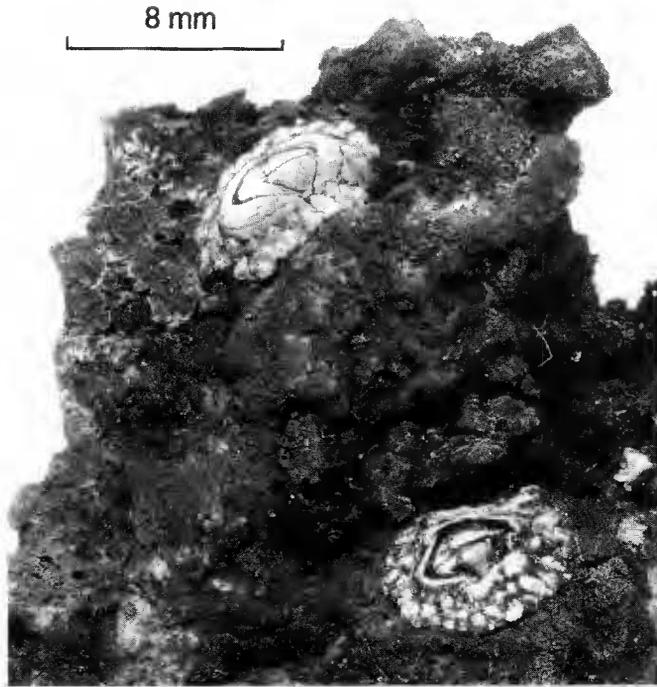


FIG. 1. — The brachylepadomorph *Neobrachylepas relicus* gen. et sp. nov. (upper, holotype) and a juvenile of the balanomorph *Eochionelasmus ohtai* Yamaguchi, 1990 (lower). The specimens, viewed from the left side, were found almost completely buried beneath sulfide and oxide deposits on a small block of basalt recovered by the French submersible *Nautille* from the hydrothermal field, Lau Basin, Tonga. The specimen of *Neobrachylepas* can be distinguished from that of *Eochionelasmus* by the more prominent carina and rostrum (C and R) which abut at their lateral margins, the pair of small latera (L) included with the operculum, and the absence of the dedicated latera (CL and RL) in the primary wall (see Fig. 2 for identification of the brachylepadomorph and Fig. 6, D1 of the balanomorph plates).

Le brachylépadomorphe Neobrachylepas relicus, n. gen., n. sp. (en haut, holotype) et un juvénile du balanomorphe *Eochionelasmus ohtai* Yamaguchi, 1990 (en bas). Les spécimens, vus du côté gauche, ont été trouvés presque complètement enfouis sous des dépôts de sulfures et d'oxydes sur un petit bloc de basalte récolté par le submersible français *Nautille* sur le site hydrothermal, Bassin de Lau, Tonga. Le spécimen de *Neobrachylepas* se distingue de celui de *Eochionelasmus* par la carina et le rostre (C et R) plus proéminents et qui se rejoignent par leurs bords latéraux, la paire de petits latera (L) inclus avec l'opercule, et l'absence de latera (CL et RL) dans la muraille primaire (voir fig. 2 pour l'identification du brachylépadomorphe et fig. 6, D1, des plaques des balanomorphes).

musculature retain a scalpellomorph facies. The scuta and terga have major and minor transverse growth ridges, but the major ones align rather than interdigitate along the occludent margin of the scuta (Fig. 2A; but see interlocking teeth below). The scuta are triangular in outline and, like the terga, are ornamented externally by longitudinal ribs. The major transverse growth lines frequently have minute pores, more or less at the intersections with the longitudinal growth lines, that in life accommodated seta. The occludent and apico-basal ridges are relatively prominent. The latter divides each scutum unequally, and the very narrow tergal portion overlaps the last increment to each of the longitudinal ribs along the scutal margin of the tergum (Fig. 3A-D). These increments coincide with a shallow, longitudinal depression on the interior of each scutum,

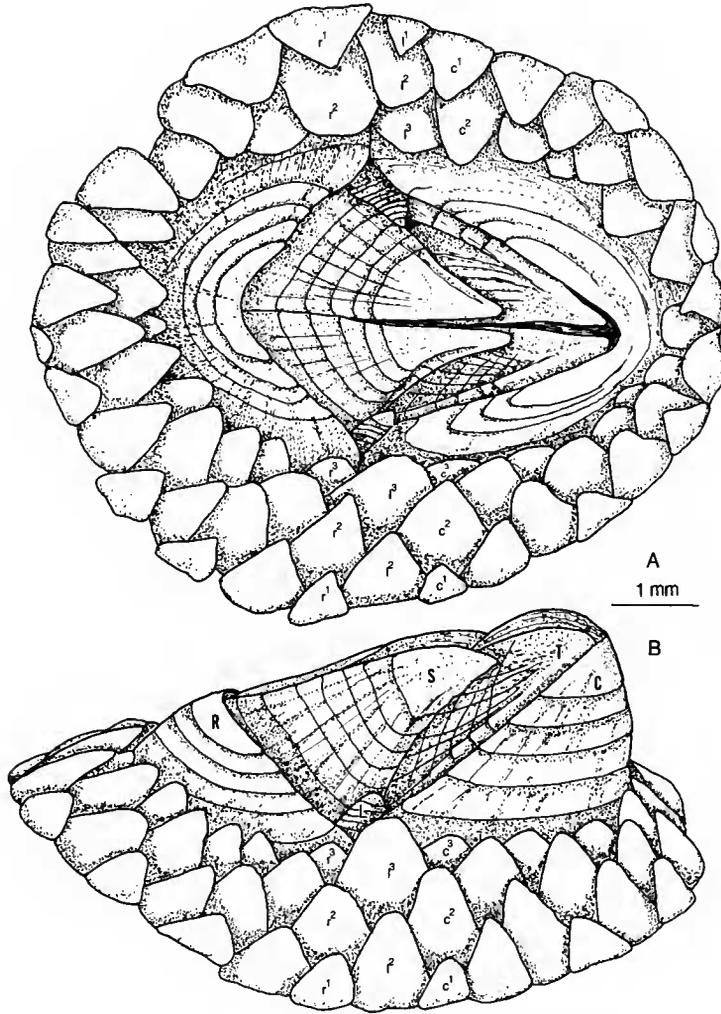


FIG. 2. — *Neobrachylepas relicha* gen. et sp. nov. Paratype 1: A, viewed from above and B, from the right side. Note that 1) the median latera (L), scuta (S) and terga (T) comprise the operculum; 2) the rostrum (R) and carina (C) are in contact at their lateral margins and there are no dedicated latera between them; and 3) while the r, l and c tiers among the imbricating plates stand three plates high on the right side (l¹ missing), and the l tier also stands three plates high on the left side, r³ and c³ of the left side have yet to appear there. The relatively large size of the left r¹ and c¹, compared to l¹ and relative to their counterparts on the right side, is puzzling.

Neobrachylepas relicha, n. gen., n. sp. Paratype 1: A, vu de dessus et B, vu du côté droit. Noter que 1) les latera médians (L), les scuta (S) et les terga (T) comprennent l'opercule; 2) le rostrum (R) et la carina (C) sont en contact par leurs bords latéraux et il n'y a pas de latera dédiés entre eux; et 3) tandis que les étages de r, l et c parmi les plaques imbriquées présentent trois plaques en hauteur du côté droit (l¹ absente), et le premier étage présente aussi trois plaques en hauteur sur le côté gauche, r³ et c³ du côté gauche restent à apparaître ici. La taille relativement grande des r¹ et c¹ gauches, par rapport à l¹ et comparée à leurs contreparties du côté droit, est surprenante.

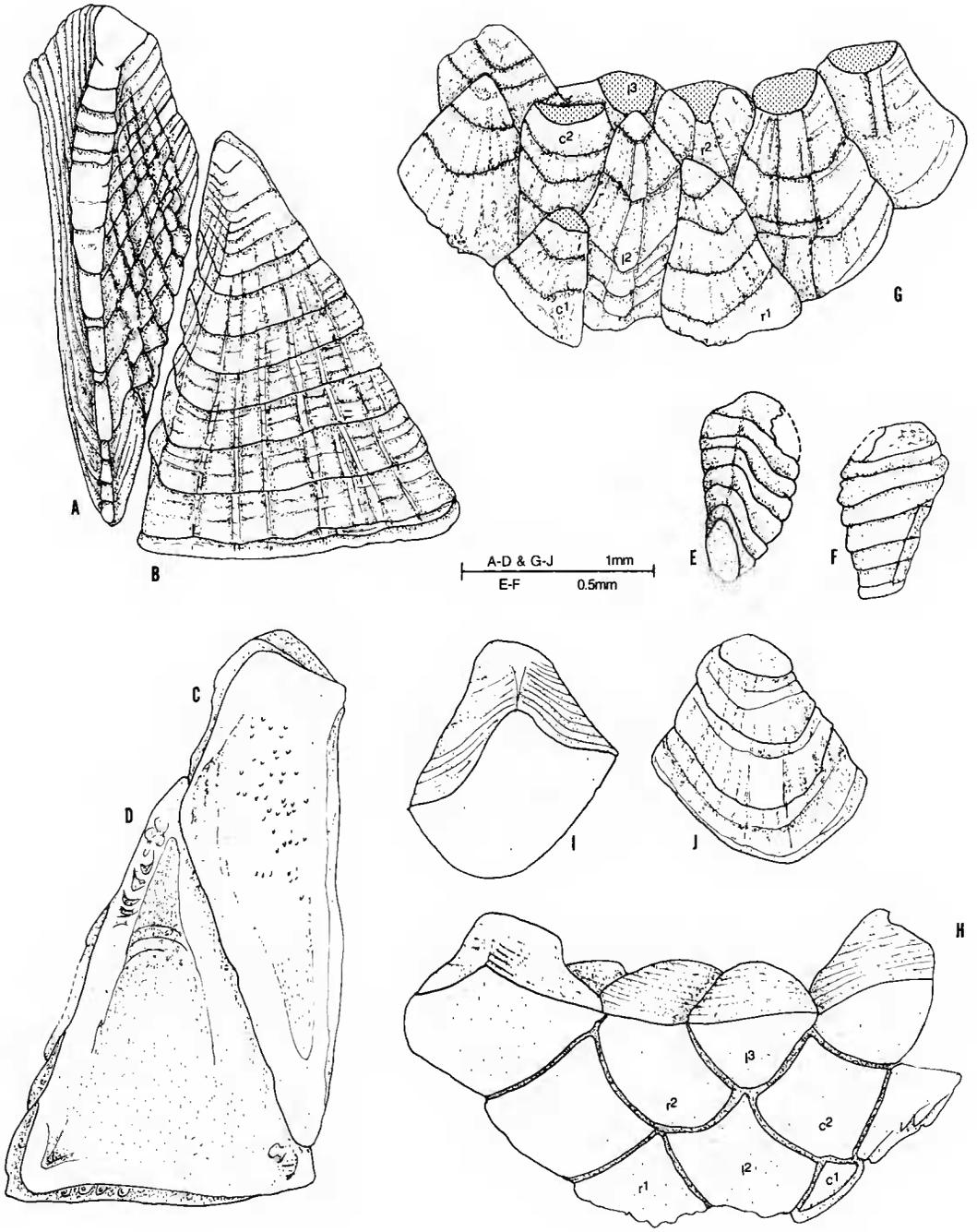
and thus the terga and scuta could be said to be slightly articulated. The interior of the scutum has a deep depression for the scutal adductor muscle, but there are no obvious depressions for insertion of rostral and lateral depressor muscles *per se*; rather, the scar for an undifferentiated sheet of depressor muscles is more or less evenly distributed on a flattened area along the basal margin, and a similar flattened area is found on the basal margin of the tergum for the insertion of the tergal depressor muscles (Fig. 3C-D). The flattened area on the scutum turns abruptly outward towards the basi-tergal angle, suggesting a different orientation of the muscle fibers inserting there (Fig. 3D). Along the upper third of the interior surface of the occludent margin of the scutum there are some irregularly spaced teeth that interdigitate with those of the opposing valve when closed, an alternate method of interlocking that has not been noted in other brachylepdomorphs, and that differs from the interdigitating of growth increments seen in many balanomorphs.

The tergum is quadrangular but unequally divided along its long axis by an apico-basal ridge (Fig. 3A). The transverse growth lines on the scutal side of the ridge are crossed by longitudinal ribs, but those of the basal portion, which are completely overlapped by the carina, are not. The central portion of the interior of the tergum is marked in its upper half by minute tubercles, and the uppermost portion of the flattened basal margin, accommodating the depressor muscles, turns abruptly inward (Fig. 3C).

The median latera are small, and reside largely on the apico-basal ridge at the basi-tergal angle of the scuta where they rest against the apico-basal ridge of the terga (Fig. 2), but whether there are lateral depressor muscles associated with them, as there likely would have been in primitive forms, was not determined. Reduction in size of the median latera, from apex to base (Fig. 3E-F), must begin early in juvenile ontogeny, likely shortly after metamorphosis from the last pedunculate to the first sessile stage (NEWMAN, 1989), whereby the median latera not only cease growing larger but actually grow progressively smaller as the animal as a whole continues to grow. Retarded development, and an occasional complete loss of the median latera, was noted in *Neoverruca brachylepadoformis* (NEWMAN, 1989), and, like the imbricating plates, it has completely disappeared in verrucids. The latera may have also disappeared in some extinct brachylepdomorphs (WITHERS, 1953), as they have in all balanomorphs (YAMAGUCHI & NEWMAN, 1990; BUCKERIDGE & NEWMAN, 1992).

The primary wall consists of the rostrum and carina surrounded by imbricating plates standing no more than three tiers (six whorls) high (Fig. 2A-B), as is the case in some brachylepdomorphs (WITHERS, 1953). Although it is possible that four tiers (eight whorls) develop in older specimens, aspects of the soft parts suggest that the wall at this stage is virtually complete.

Formerly the uppermost imbricating plates in the tiers of “sublatera” (WOODWARD, 1901), in proverrucids and neoverrucids (NEWMAN & HESSLER, 1989) as well as brachylepdomorphs (NEWMAN, 1987), were considered homologous with the rostralateral and carinolateral plates of the pollicipedine scalpellomorphs and the balanomorphs. These were distinguished from other latera in their respective tiers by the use of upper rather than lower case lettering (RL-CL rather than rl-cl or r-c; NEWMAN, 1987). This convention was initiated at a time when it was thought that imbricating whorls in *Brachylepas* were added peripherally, as in pollicipedines and primitive balanomorphs. With knowledge of the ontogeny of *Neoverruca* (NEWMAN, 1989) it became apparent that they were added in the reverse order in neoverrucids and likely in brachylepdomorphs,



and from the present material this is evidently the case. Thus, it is equivocal which latera of the r and c tiers in brachylepadorphs and verrucomorphs are homologous with RL and CL in pollicipedines and balanomorphs, and therefore the usage of the upper case designation is suppressed here (Figs 2, 3G-H).

The imbricating plates of the first paratype, rostrad and carinad of the median lateral tiers, comprise some 14 and 16 tiers, respectively (Fig. 2A), the sum of which, including the median lateral tiers, comes to 32 tiers in all (the holotype appears to have only 30 tiers). This is essentially 10 tiers less than seen in the much larger species, *Brachylepas cretacea* (see NEWMAN, 1987). No subcarinal or subrostral (sc and sr) tiers were identifiable although, judging from the ontogeny of *Neoverruca* (NEWMAN, 1989), they are likely present in the earliest ontogenetic stages. The three sublateral tiers (labeled simply r, l and c, rather than rl, l and cl, herein) not only tend to include the largest latera (especially those of the l tier), but to stand three rather than two plates high (Fig. 2).

Externally the individual imbricating plates are marked by strong transverse growth lines and relatively weak apico-basal ribs, the essentially median one sometimes being stronger (Fig. 3G, l² and r² for example), but otherwise they look much alike.

When viewed from within, three patterns are observed:

- 1) the plates of uppermost whorl which are overlapped but do not yet overlap adjacent plates;
- 2) the uppermost plates that overlap but one adjacent plate;
- 3) the plates that overlap two plates (Fig. 3, l³, r² and l², respectively).

All plates retain the first pattern unless they come to overlap plates of subsequent whorls. A few may retain the second pattern, but most progress to the third pattern during ontogeny.

The lateral margins of the rostrum and carina are in contact, but whether they will remain so with subsequent growth is unknown. Their outer surfaces are marked by prominent transverse growth lines and weak apico-basal ridges (Fig. 2) and the slight depressions between the latter correspond to the number of tiers, which is 32 in the first paratype. Thus the tiers correspond to the grooves, rather than to the ribs as they do in *Brachylepas cretacea* (see NEWMAN, 1987). There is a median sagittal ridge rather than a depression on both the rostrum and carina, again indicating that if there were subrostral and/or subcarinal tiers of plates, they lost their identity as such early in ontogeny.

FIG. 3. — *Neobrachylepas relicha* gen. et sp. nov. Paratype 1: A-B, external and C-D, internal views of left tergum and scutum, respectively; E-F, internal and external views of right median latus (twice the magnification of the other plates); G-H, external and internal views of a group of imbricating plates including the r-l-c tiers of the left side (l¹ illustrated in Fig. 1 missing, uniform stippling indicates where the tops of some plates in G have been eroded and/or broken off); I-J, internal and external views of an imbricating plate.

Neobrachylepas relicha, n. gen., n. sp. Paratype 1: A-B, vue externe et C-D, vue interne des tergum et scutum gauches, respectivement; E-F, vues interne et externe du latus médian droit (grossissement double des autres plaques); G-H, vues externe et interne d'un groupe de plaques imbriquées incluant les étages r-l-c du côté gauche (l¹ illustré sur la fig. 1 absent, le pointillé uniforme indique les sommets de certaines plaques de G qui ont été érodées et/ou cassées); I-J, vues interne et externe d'une plaque imbriquée.

Soft parts

The trophi (Fig. 4A-D) are very similar to those of other hydrothermal vent barnacles, reflecting adaptations to feeding on very fine particles, presumably small, suspended clumps of bacteria. The slightly bullate, unnotched labrum of *Neobrachylepas relicca* (Fig. 4A) supports relatively large palps provided with relatively stout setae and, on the posterior (inner) surface, in addition to the usual row of very fine teeth there are long fine setae on each side of the midline directed toward the mouth. The mandible (Fig. 4B) is characteristic of hydrothermal vent forms; one superior incisiform tooth followed by three teeth each supporting a row of short sharp spines along the superior curvature, several of the uppermost of which roll over onto the posterior surface, and an inferior angle supporting a row of similar spines.

In some hydrothermal vent forms the division between the last spine of the fourth tooth and the first spine, on the outer margin of the inferior angle of the mandible, can be obscure. Here it is indicated by a slight enlargement of the first few spines belonging to the inferior angle. The mandibles of *Neobrachylepas* and *Neoverruca* are distinguished from those of other hydrothermal forms in having a single row of setae between the first and second teeth.

Maxillae I and II (Fig. 4C-D) each support a relatively uniform comb of slender setae and are undistinguished from other vent forms.

Cirri I, with the proximal segments of both rami lobate and densely setose and the distal articles antenniform and sparsely setose, are similar to those of other vent species. However, in *Neobrachylepas* the change from lobate to antenniform is remarkably abrupt (Fig. 4E). The setation of the antenniform and lobate articles is depicted in Fig. 4F, G, respectively. Cirri II (Fig. 4H) are remarkable in both rami being relatively short and neither being antenniform, but antenniformity is known to vary in other barnacles. An extension of the testes occupies the coxal segment of the pedicle and, while another although smaller branch also occurs in cirrus III, none were observed in the remaining cirri. The rami of cirri III-VI are long and ctenopod, with a number of fused basal segments followed by initially short and then longer articles (Fig. 5B-C, respectively). The rami of cirri V and VI were tightly coiled, making it difficult to count the number of articles as noted in the following (a/p = segment counts for anterior/posterior rami, and c.a. for the caudal appendages):

Cirrus	I	II	III	IV	V	VI	c.a.
a/p	32/27	9/9	20 ⁺ /38	32/38	~ 49	~ 53	1

The caudal appendages, absent in *Neoverruca* and multiarticulate in *Eochionelasmus*, are minute and unarticulate in *Neolepas* and in *Neobrachylepas* (fig. 5A & D). The penis is long, conspicuously annulated, and sparsely clothed with short, stiff setae (Fig. 5A, E, F).

A unique feature, known in no other cirriped, is a median “dorsal” appendage (Fig. 5G) located on the prosoma somewhat anterior to the position of the maxillary segment. It consists of a stiff tapering rod sparsely clothed with basally directed barbs and terminating in a tuft of short, stiff setae. It is in a position to become surround by an egg lamella when laid and to retain it against the dorsum during brooding. But whether ovigerous frena (WALKER, 1983),

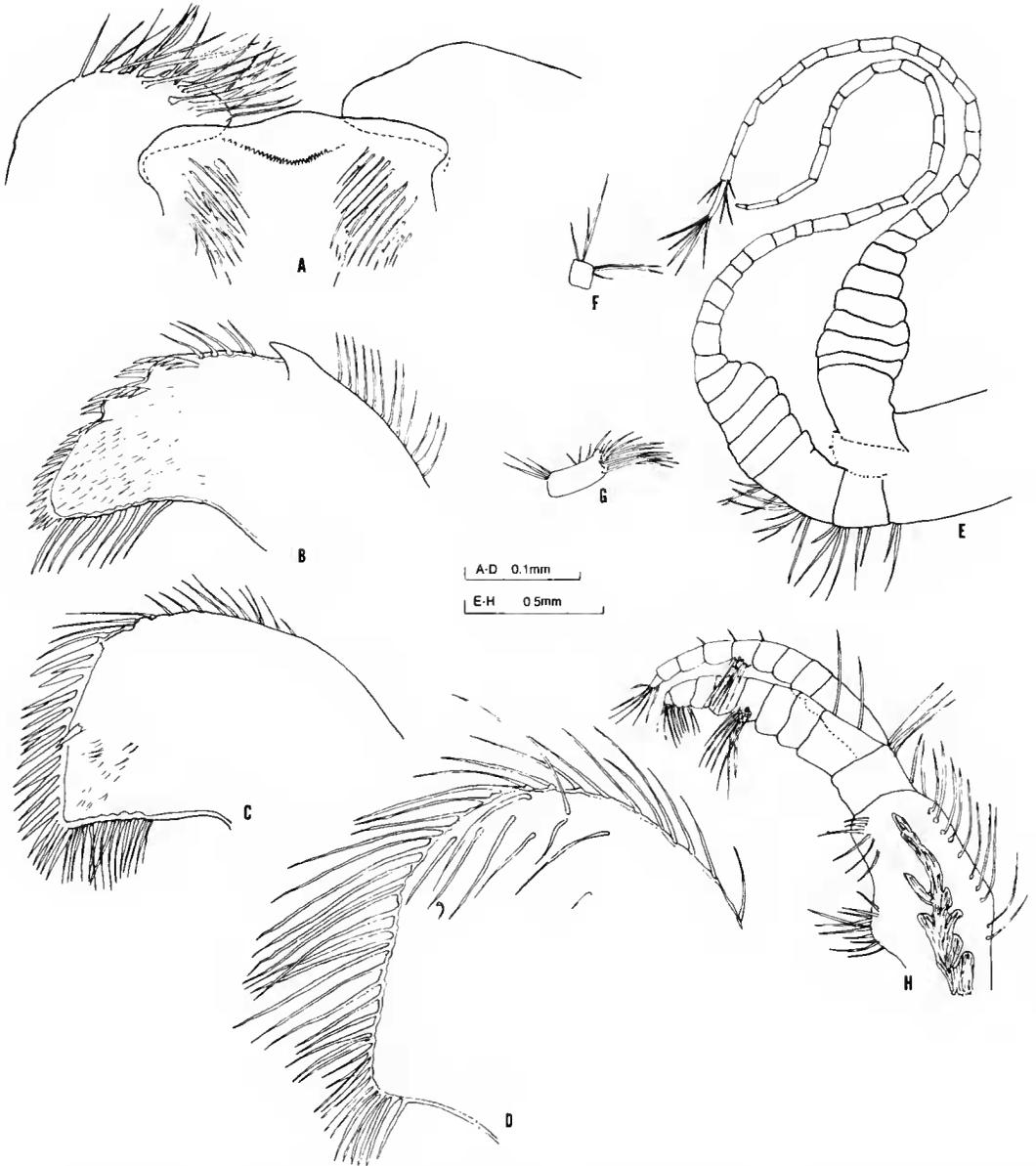


FIG. 4. — *Neobrachylepas relicha* gen. et sp. nov. First paratype; trophi and cirri I-II: A, labrum and palps (seta on right palp omitted); B, C and D, right mandible, maxilla I, and maxilla II, respectively; E, right cirrus I (most setae omitted, posterior ramus partially torn from pedicle); F & G, articles 5 and 10 of anterior ramus of cirrus I (counting the 3 fused basal segments as 1); H, right cirrus II (with setation shown on articles 4 and 5 of the outer and inner rami, respectively).

Neobrachylepas relicha, n. gen., n. sp. Paratype 1; appendices buccaux et cirres I-II: A, labre et palpes (soies omises sur le palpe droit); B, C et D, mandibule droite, maxille I et maxille II, respectivement; E, cirre I droit (la plupart des soies omises, rame postérieure partiellement arrachée du pédicule); F et G, articles 5 et 10 de la rame antérieure du cirre I (en comptant pour un les 3 segments basaux fusionnés); H, cirre 2 droit (avec sétation présente sur les articles 4 et 5 des rames externe et interne, respectivement).

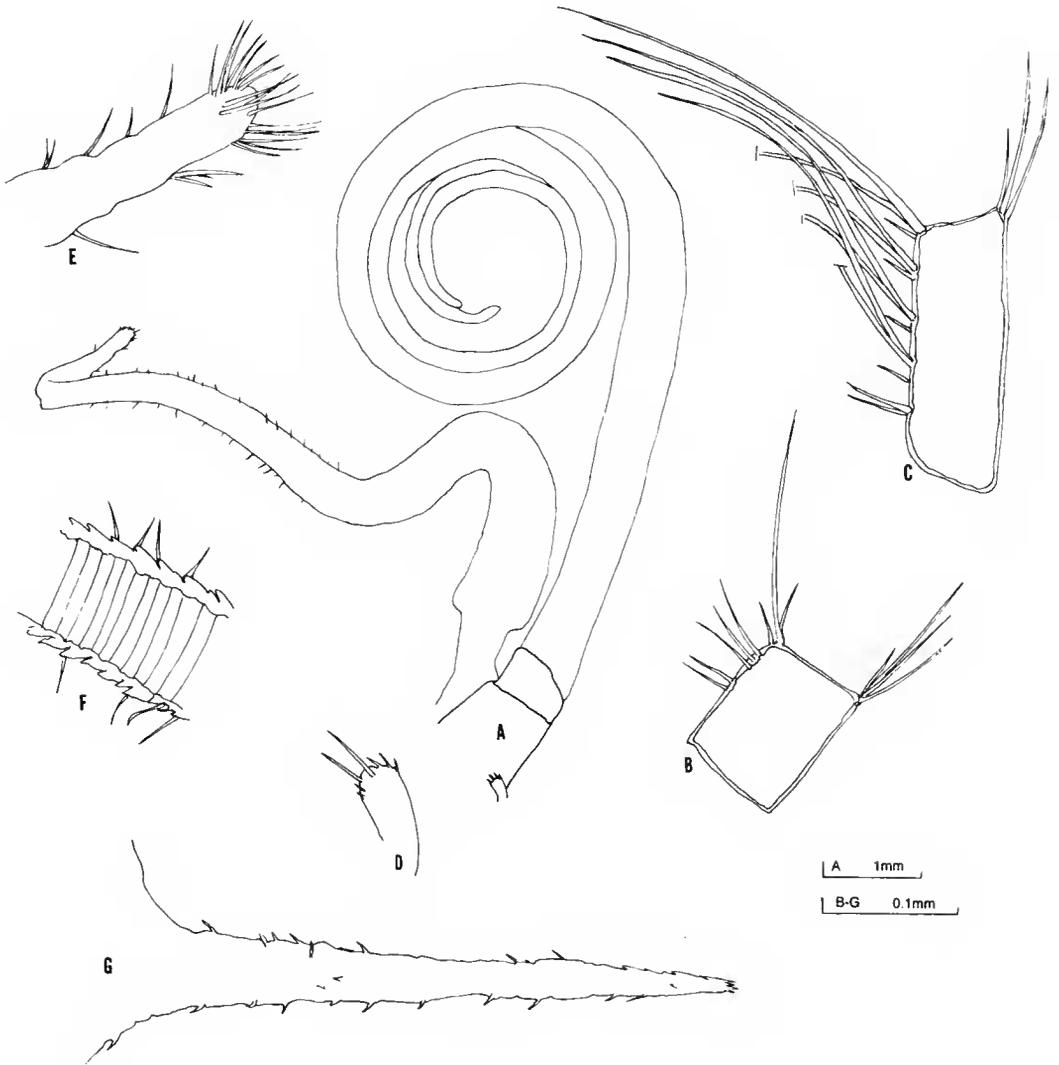


FIG. 5. — *Neobrachylepas relicus* gen. et sp. nov. First paratype: A, right cirrus VI (setae omitted), penis, and caudal appendage; B and C, articles from the lower and upper third of the inner ramus of cirrus VI, respectively (some setae cut short in latter); D, left caudal appendage enlarged; E and F, apex and central section of the penis enlarged; G, median dorsal appendage.
Neobrachylepas relicus, n. gen., n. sp. Paratype 1: A, cirre VI, droit (soies omises), pénis et appendice caudal; B et C, articles des tiers supérieur et inférieur de la rame interne du cirre VI, respectivement (quelques soies raccourcies sur ce dernier); D, appendice caudal gauche agrandi; E et F, apex et section centrale du pénis agrandis; G, appendice dorsal médian.

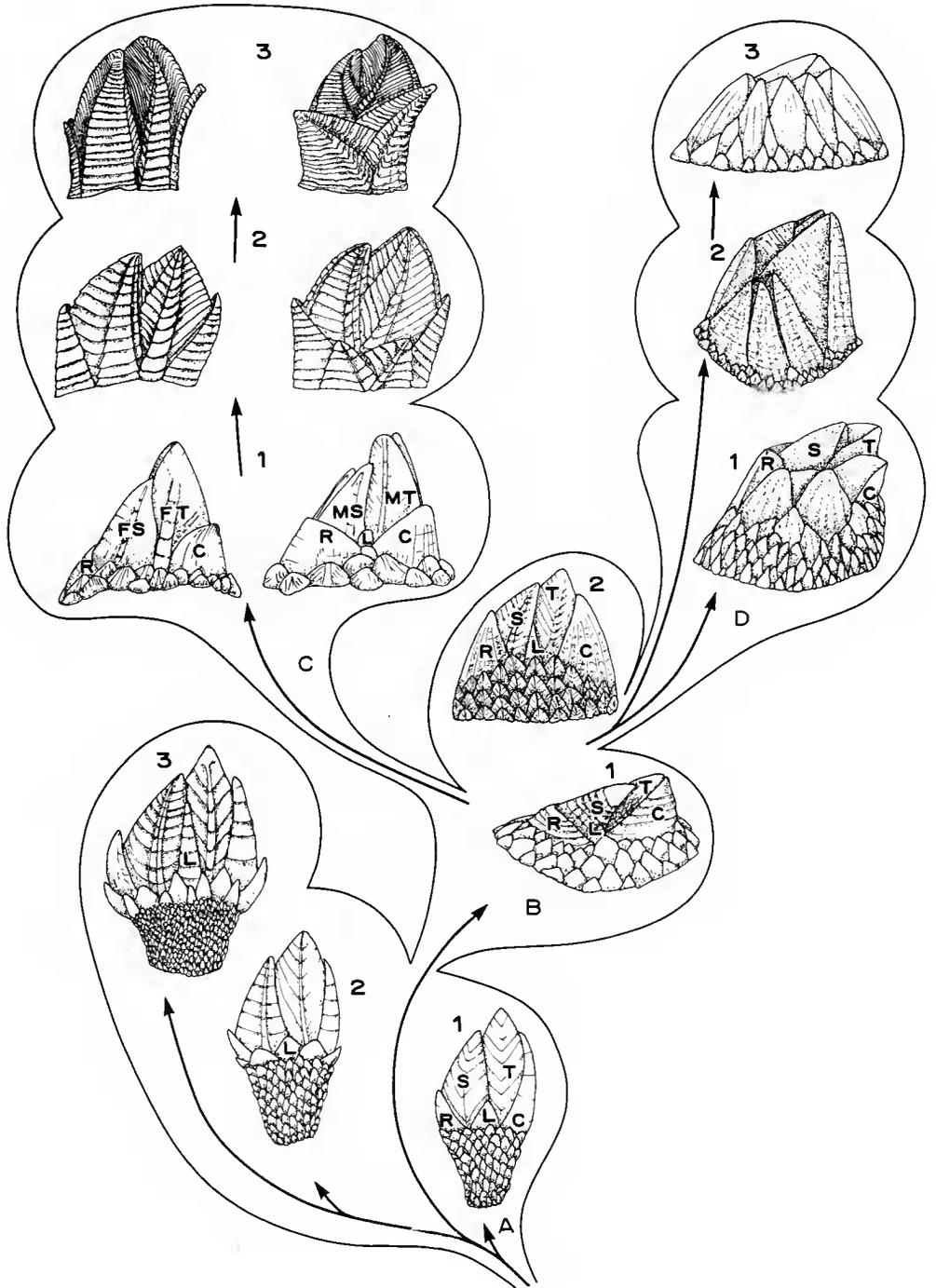
present in *Neolepas* and *Neoverruca*, are absent in *Neobrachylepas* was not determined. *Neoverruca* has a similarly positioned median dorsal organ, but it qualifies as a “filamentary” appendage in being thin-walled, soft, flexible and without setae, and in containing ramifications of the testes, as do some such filamentary appendages in some pedunculate barnacles (DARWIN, 1852). In addition to that seen in *Neoverruca*, prosomal dorsal filamentary appendages, including a small median one, are also known in some *Scillaelepas* (NEWMAN, 1980), and it is from such a precursor that the median dorsal appendage seen in *Neobrachylepas* likely evolved.

AFFINITIES

The morphology of the hard parts in *Neobrachylepas relicha* is unique among living barnacles, yet its trophi and cirri are specialized in the same way as in the other hydrothermal vent barnacles, even though they belong to distinct suborders (NEWMAN, 1979; NEWMAN & HESSLER, 1989; YAMAGUCHI & NEWMAN, 1990; JONES, 1993). The similarity, the result of adaptations to feeding on very fine particles, points to the need for caution in using general aspects of the trophi and cirri in considerations of affinity.

The unique organization plan of the shell distinguishes *Neobrachylepas relicha* from all living barnacles, and if it were not for the fossil record we would be hard pressed of what to make of it. Fortunately there is a part for part correspondence between WOODWARD's reconstruction of *Brachylepas cretacea* from the Norwich Chalk (WOODWARD, 1901) and *Neobrachylepas* (compare Fig. 6B1-2). Prior to the discovery of the vent species, the Brachylepadomorpha included *Brachylepas* (Upper Cretaceous) and *Pycnolepas* (Upper Jurassic-Upper Miocene; NEWMAN *et al.*, 1969; COLLINS, 1980; ZULLO *et al.*, 1987), and reconstructions of both genera have high-standing, scalpellomorph- rather than balanomorph-like opercular plates (WOODWARD, 1901; WITHERS, 1923; Fig. 6B2). *Neobrachylepas* differs from the foregoing genera in a number of characters, and the balanomorph-like stance of the opercular valves is particularly obvious (compare Fig. 6B1 versus B2 and D1-3 for examples). In addition, it differs in being peltate rather than high-conical, in the carina and rostrum abutting at their lateral margins rather than being separated by the sublatera, and in the lowermost imbricating whorls lacking interlocking mortises and tenons between the plates. And it may also differ from most brachylepadomorphs in the median three tiers of imbricating plates standing three rather than four plates high.

All of these shell characters, including small size, could be because the largest specimens available are juveniles. While confirmation of adult characters awaits the discovery of an ovigerous specimen, the soft parts of paratype 1 revealed mature male organs (penis and testes) and a median dorsal appendage that apparently holds an ovigerous lamella in place while brooding. Thus, other than for the production of eggs, this specimen appears mature and, therefore, substantial ontogenetic changes in the structure of the shell seem unlikely. Continued growth could result in a thicker and likely less peltate wall, and perhaps the addition of as many as two more whorls of imbricating plates. But it is deemed unlikely that the stance of the opercular valves would change much if at all because it would require a substantial change in the otherwise narrow form of the basal margin of the tergum, and because it would be disadvantageous in an environment where crushing predators such as crabs exist.



THE SESSILE BARNACLES

The sessile barnacles are treated here (Figs 6-7) as monophyletic (NEWMAN, 1987, 1993). Although ANDERSON (1994) continues to embrace diphyly, nothing compelling has been added to earlier views on the matter (NEWMAN & ROSS, 1976; NEWMAN, 1982, 1987; ANDERSON, 1983) and therefore the argument is not reconsidered here.

There has been no doubt since DARWIN (1854) that the scalpellomorphs gave rise to the sessile barnacles (ANDERSON, 1983; NEWMAN, 1993). It has been demonstrated that the first sessile barnacles, the Brachylepadomorpha, differ from the scalpellomorphs in that the capitulum and peduncle cease to exist as such during early ontogeny (NEWMAN, 1989).

Each becomes divided into new structures, e.g.:

- 1) a movable operculum consisting of the scuta and terga derived from the capitulum and a pair of latera derived from the peduncle;
- 2) a wall consisting of the carina and rostrum derived from the capitulum reinforced by whorls of imbricating plates derived from the peduncle;
- 3) a membranous or calcareous basis derived from the peduncle.

FIG. 6. — Affinities of the Scalpellomorpha (A) and the Sessilia (B-D). The most primitive living members of the suborders Scalpellomorpha, Verrucomorpha, and Balanomorpha, and the only living member of the Brachylepadomorpha (A1, B1, C1 and D1) are known from hydrothermal vents (modified from NEWMAN & HESSLER, 1989; YAMAGUCHI & NEWMAN, 1990; BUCKERIDGE & NEWMAN, 1992): A) Scalpellomorpha in part: 1) *Neolepas zeviniae* from hydrothermal vents at 2600 m, Eastern Pacific (NEWMAN, 1979); 2) *Scillaelepas*, deep-water, 400-2000 m (NEWMAN, 1980); and 3) *Capitulum mitella*, intertidal, West Pacific (NEWMAN, 1987). B) Brachylepadomorpha in part: 1) *Neobrachylepas relicha* gen. et. sp. nov., 1900 m, Lau Basin, Tonga; 2) *Brachylepas cretacea*¹, Upper Cretaceous, England (modified from WOODWARD, 1901; WITHERS, 1935; NEWMAN, 1987). C) Verrucomorpha in part: 1) *Neoverruca brachylepadiformis*², 3600 m, Marina Back-Arc Basin (NEWMAN & HESSLER, 1989); 2) *Eoverruca hewitti*, Upper Cretaceous, England (WITHERS, 1935); and 3) *Verruca*, cosmopolitan, mostly deep water to approximately 5000 m. D) Balanomorpha in part: 1) *Eochionelasmus ohtai*, 1990 m, North Fiji Basin (YAMAGUCHI & NEWMAN, 1990); 2) *Waikalasma juneae*, Upper Miocene, New Zealand (BUCKERIDGE, 1983), and 3) a generalized *Catophragmus*³, extant species intertidal, Bermuda and Caribbean Islands, off-shore islands on the Pacific side of Panama and Costa Rica, and Southeast Australia and Tasmania (DARWIN, 1854; STANLEY & NEWMAN, 1980).

1. For simplicity, some tiers of imbricating plates on either side of the medial three have been omitted. 2. Verrucomorphs can be either right- or left-sided. Both the movable side (MS-MT) and the fixed side (FS-FT) of each species is illustrated from the right side here (e.g., one or the other is a mirror image) so that the asymmetry can be easily compared. 3. For simplicity, the number of whorls of imbricating plates has been reduced to three.

Affinités des Scalpellomorpha (A) et des Sessilia (B-D). Les membres vivants les plus primitifs des sous-ordres Scalpellomorpha, Verrucomorpha et Balanomorpha, ainsi que l'unique représentant vivant des Brachylepadomorpha (A1, B1, C1 et D1) sont connus des sources hydrothermales (modifié d'après NEWMAN & HESSLER, 1989; YAMAGUCHI & NEWMAN, 1990 et BUCKERIDGE & NEWMAN, 1992) : A) Scalpellomorpha (part.) : 1) Neolepas zeviniae des sources hydrothermales à 2 600 m de profondeur, Pacifique oriental (NEWMAN, 1979) ; 2, Scillaelepas, eaux profondes, 400-2 000 m (NEWMAN, 1980) et 3) Capitulum mitella, intertidal, Pacifique occidental (NEWMAN, 1987) ; B) Brachylepadomorpha (part.) : 1) Neobrachylepas relicha, n. gen., n. sp., 1 900 m, Bassin de Lau, Tonga ; 2) Brachylepas cretacea¹, Crétacé supérieur, Angleterre (modifié d'après WOODWARD, 1901 ; WITHERS, 1935 ; NEWMAN, 1987) ; C) Verrucomorpha (part.) : 1) Neoverruca brachylepadiformis², 3 600 m, arc postérieur du Bassin Marina (NEWMAN & HESSLER, 1989) ; 2) Eoverruca hewitti, Crétacé supérieur, Angleterre (WITHERS, 1935) et 3) Verruca, cosmopolite, habituellement en eaux profondes jusqu'à environ 5 000 m ; D) Balanomorpha (part.) 1) Eochionelasmus ohtai, 1 990 m, Bassin du nord des Fidji (YAMAGUCHI & NEWMAN, 1990) ; 2) Waikalasma juneae, Miocène supérieur, Nouvelle-Zélande (BUCKERIDGE, 1983) et 3) un Catophragmus³ généralisé, espèce actuelle intertidale, Bermudes et Caraïbes, îles au large de la côte Pacifique de Panama et Costa Rica, et Australie du sud-est et Tasmanie (DARWIN, 1854 ; STANLEY & NEWMAN, 1980).

1. Pour simplifier, certains étages de plaques imbriquées de chaque côté des trois médians ont été omis. 2. Les verrucomorphes présentent une asymétrie droite ou gauche. Le côté mobile (MS-MT) et le côté fixe (FS-FT) de chaque espèce sont l'un et l'autre illustrés ici du côté droit (c'est-à-dire, l'un ou l'autre est une image miroir) si bien que l'asymétrie peut être facilement comparée. 3. Pour simplifier, le nombre de tours de plaques imbriquées a été réduit à trois.

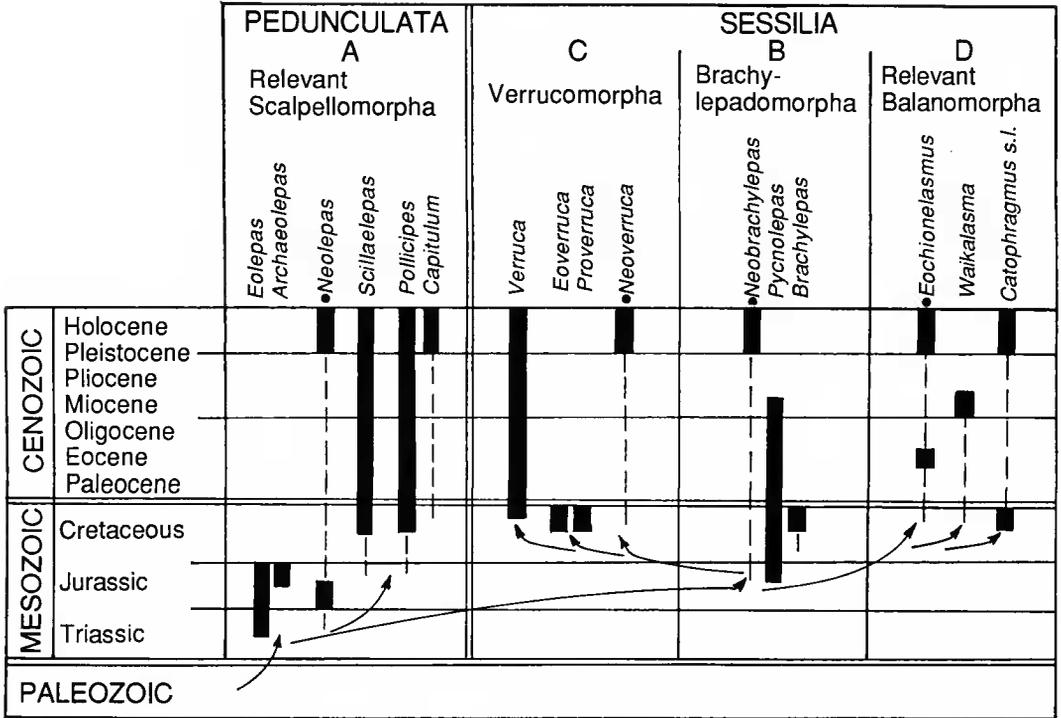


FIG 7. — Geological ranges of early sessile barnacles among the Brachylepadomorpha, Verrucomorpha and relevant Balanomorpha, and the relevant pedunculate lineage within the Scalpellomorpha (modified from NEWMAN & HESSLER, 1989). Vertical bars and dashed lines represent the known and inferred ranges, respectively [The range for *Neolepas* is inferred from knowledge of a similar form from the Lower Jurassic of New Caledonia (BUCKERIDGE & GRANT-MACKIE, 1985), and the Eocene record for *Eochionelasmus* is inferred from Eocene records for *Chionelasmus* from Tonga (STANLEY & NEWMAN, 1980; YAMAGUCHI & NEWMAN, 1990) and the Chatham Islands (BUCKERIDGE, 1985). Genera preceded by a dot are not only the most primitive or sole surviving members of their suborders but they are hydrothermal vent endemics.

Répartition géologique des premiers cirripèdes parmi les Brachylepadomorpha, les Verrucomorpha et les Balanomorpha concernés ainsi que la lignée des pédonculés chez les Scalpellomorpha (modifié d'après NEWMAN & HESSLER, 1989). Les barres verticales et les lignes en pointillés représentent respectivement la répartition connue et supposée. La répartition de Neolepas est déduite de la connaissance d'une forme similaire du Jurassique inférieur de Nouvelle-Calédonie (BUCKERIDGE & GRANT-MACKIE, 1985) et la mention de l'Eocène pour Eochionelasmus est déduite des mentions de l'existence à l'Eocène de Chionelasmus de Tonga (STANLEY & NEWMAN, 1980; YAMAGUCHI & NEWMAN, 1990) et des îles Chatham (BUCKERIDGE, 1985). Les genres précédés d'un point ne sont pas seulement les plus primitifs ou les seuls membres survivants de leurs sous-ordres mais ils sont aussi des genres endémiques des sources hydrothermales.

Therefore the operculum and wall are new, compound structures; there is no capitulum or peduncle *per se* in adult sessile barnacles, and to avoid confusion the nomenclature should be avoided in discussing adult sessile barnacle morphology.

The brachylepadomorphs appeared in the Upper Jurassic, more than 50 million years before the appearance of the verrucomorphs and balanomorphs (WITHERS, 1935; NEWMAN *et al.*, 1969; Fig. 7B versus C-D). There is presently no question that the brachylepadomorphs gave rise to the asymmetrical sessile barnacles, the Verrucomorpha (NEWMAN, 1987, 1989; NEWMAN &

HESSLER, 1989). The basic neoverrucid differs from the brachylepadomorphs in having one side of the otherwise movable operculum incorporated into the wall (Fig. 6, B1 and 2 to C1; NEWMAN & HESSLER, 1989).

The brachylepadomorphs are also inferred to have given rise to the higher symmetrical sessile barnacles, the balanomorphs, and the differences between *Eochionelasmus* and *Neobrachylepas* have already been noted (Fig. 1; YAMAGUCHI & NEWMAN, 1990). The extinct (Miocene) balanomorph, *Waikalasma* (BUCKERIDGE, 1983; BUCKERIDGE & NEWMAN, 1992) and the predominantly intertidal balanomorph, *Catophragmus* s.l. (DARWIN, 1854), with its relict populations in a few places in the world (STANLEY & NEWMAN, 1980), are even more highly organized than *Eochionelasmus* (compare Fig. 6, D1-D3) and, therefore, bear on the radiation rather than the origin of balanomorphs.

The primitive balanomorphs differ fundamentally from both the brachylepadomorphs and the verruciforms in having at least two pairs of lateral plates incorporated into the wall (YAMAGUCHI & NEWMAN, 1990; Fig. 6D-1) and, during ontogeny, in adding successive whorls of imbricating plates outside rather than inside of the preceding whorl (NEWMAN, 1989). The incorporation of latera into the primary wall poses no more theoretical difficulties than the incorporation of the median latus into the operculum, but reversal in the order of addition of imbricating plates necessary to convert a brachylepadomorph into a balanomorph wall, might seem to. However, the explanation is the same as that for the origin of the capitular imbricating plates in scalpellomorphs; *e.g.*, there are effectively two bands of hypodermis in the plate-producing zone between the capitulum and the peduncle, one secreting the plates of the former and the other those of the latter (DARWIN, 1852). Now, considering metamorphosis from the last pedunculate juvenile stage to the first sessile stage, known in *Neoverruca* and inferred in brachylepadomorphs (NEWMAN, 1989), if the band that secreted the first whorl of imbricating plates were to secrete the second and subsequent whorls outside rather than inside the previous whorl, the balanomorph level of organization would have been achieved. Such a reversal must have taken place in reaching the pollicipedine level of organization, and therefore hypothesizing such a reversal in the evolution of the earliest balanomorph is reasonable. Once established, the latera immediately overlapping the space between the rostrum and carina remain in place rather than being displaced basalwards by the next whorl to be added. Therefore, they are in a position to be incorporated into the primary wall. Ontogenetic evidence suggests that the first to be incorporated were cl^1 and rl^1 , in that order (NEWMAN, 1989), and once so dedicated they can be designated CL and RL (YAMAGUCHI & NEWMAN, 1990; BUCKERIDGE & NEWMAN, 1992; NEWMAN, 1993).

ANTIQUITY

The life of individual vents can be relatively short, in terms of decades or less, and the spatial and temporal intensity of hydrothermal activity in general has apparently varied considerably throughout the Phanerozoic (HESSLER & LONSDALE, 1991). Therefore, the probability of extinction would seem relatively high (NEWMAN, 1979; TUNNICLIFFE, 1992). As a result, there have been two schools of thought concerning the age of ancient-appearing forms found associated with vents (NEWMAN, 1985). While most people take the evidence for primitiveness, and therefore great age, at face value, there are some who believe that vents are too ephemeral to act as

refugia for vestiges of ancient lineages, and they suggest that what similarities there may be between vent inhabitants and extinct forms may have been recently acquired through retrogressive evolution (COHEN & HAEDRICH, 1983; HICKMAN, 1984; MCLEAN, 1988).

Barnacles can be useful in resolving such matters because the ontogenies as well as morphologies of many living forms are relatively well known, they have reasonably well documented fossil records, and their general evolution is fairly well understood. Therefore an adult morphology without a fossil record can often be assigned a geologic age (NEWMAN, 1985), and by this measure alone the obligate vent barnacles reported to date are largely Mesozoic.

The organization plan of the plates of the first vent barnacle discovered, the scalpellomorph *Neolepas*, lacked a fossil record when first discovered, but a Mesozoic age (Upper Jurassic) was inferred from the ontogeny and fossil record for related forms (NEWMAN, 1979). This age has, in effect, been corroborated by the recognition of a neolepadine from the Lower Jurassic of New Caledonia (BUCKERIDGE & GRANT-MACKIE, 1985). However, the organization plan of *Neolepas* itself conceivably could have resulted from retrogressive evolution (progenesis) because a *Neolepas*-like morphology appears in the ontogeny of scalpellomorphs, such as extant *Scillaelepas* in the surrounding deep sea, and this supposition weakens the inference for a Mesozoic age and entry into the vent refugium.

More compelling evidence for a predominantly Mesozoic age for the vent fauna came with the discovery of the second vent barnacle, the verrucomorph *Neoverruca* (NEWMAN & HESSLER, 1989). It is more compelling because, while also lacking a fossil record, there is neither an extant verrucomorph nor a known ontogeny from which a neoverrucid could have evolved by retrogressive evolution. Furthermore, *Neoverruca* not only represents the most primitive living verrucomorph but essentially the missing link between the Brachylepadoromorpha and the Verrucomorpha, a radiation that apparently was completed in the Cretaceous (SCHRAM & NEWMAN, 1980). Therefore, *Neoverruca* appears to be a Mesozoic relic *par excellence*.

If the previous example was more compelling, it was by no means as compelling as the third and fourth. Like the first two, the third vent barnacle to be discovered, the balanomorph *Eochionelasmus*, is considered to be the most primitive living member of its suborder (YAMAGUCHI & NEWMAN, 1990) and, instructively, the Balanomorpha also appeared, albeit late, in the Cretaceous. Thus it would seem that the Mesozoic nature, of at least the barnacles of hydrothermal vents, had been well corroborated (YAMAGUCHI & NEWMAN, 1990; BUCKERIDGE & NEWMAN, 1992). But the most compelling case, the subject of the present report, was yet to come.

The fourth vent barnacle, *Neobrachylepas*, belongs to the most primitive and oldest suborder of the sessile barnacles, the Brachylepadoromorpha. The brachylepadoromorphs, which appeared in the Jurassic, were thought to have died out in the Miocene, while the other three suborders, Scalpellomorpha, Verrucomorpha and Balanomorpha, range on to the Recent (NEWMAN *et al.*, 1969). The imbricating whorls of plates making up the lower portion of the wall of *N. relicae* are the most generalized known from the brachylepadoromorphs and therefore it presumably has descended from an early lineage that entered the hydrothermal environment in the Late Mesozoic, conceivably as early as the Upper Jurassic.

The earliest members of suborders Scalpellomorpha, Verrucomorpha, Brachylepadoromorpha and Balanomorpha, which the contemporary vent barnacles are known or inferred to resemble, would have been available to enter the hydrothermal environment between the Lower Jurassic

and the Upper Cretaceous. Since there is no evidence that any forms resembling those presently found associated with vents and cognate environments persisted into the Tertiary outside of such environments, the most defensible hypothesis is that the association was made at least by the end of the Cretaceous.

ORIGINS

No hydrothermal barnacles are known from Atlantic vents (SEGONZAC, 1992), nor from the Galapagos vents for that matter, despite a reasonable sampling effort (TUNNICLIFFE, 1991). The vent scalpellomorph, *Neolepas*, first reported from the East Pacific (NEWMAN, 1979; Fig. 6, A-1; 10°N to 21°N), is now known by a similar form at 23°S in the East Pacific (JONES, 1993) and by a number of related West Pacific forms from vents near Tonga, Fiji and Manus to as far north as Okinawa (unpubl.). Similarly, neoverrucids are widely distributed in the western Pacific, both north and south of the equator, although none are known from the eastern Pacific. The balanomorph, *Eochionelasmus ohtai*, is known from Fiji and Tonga (YAMAGUCHI & NEWMAN, 1990) and from Manus Basin to the west (TUFAR, 1990; GALKIN, 1992a, b), and an undescribed species of the genus is known from 17°S near Easter Island in the east (unpubl.), but none are known from the northern hemisphere. The remaining sessile vent barnacle, the brachylepadomorph *Neobrachylepas relicha* nov., is from Lau. Therefore, it is instructive to note that, just as with the shallow-water fauna, the western Pacific, especially the Southwest Pacific, encompasses a greater diversity of Mesozoic marine relics seen anywhere in the world (NEWMAN, 1991).

It is not surprising that barnacles are found in a severe ecotone such as hydrothermal vents because they are known to be tolerant of severe conditions such as the intertidal (YAMAGUCHI & NEWMAN, 1990). Nor is it surprising that they represent primitive forms because ecotones that persist for extended periods of time commonly constitute refugia, and the hydrothermal one has apparently been in existence throughout at least the Phanerozoic (CORLISS *et al.*, 1979; TUNNICLIFFE, 1991). But that they should represent primitive members of lineages appearing in a relatively narrow window of the Mesozoic (Fig. 6) is not only remarkable but likely more than simply coincidental.

The Upper Mesozoic, especially the Cretaceous, was the period in which the dominance of the high-profile, heavily armored pedunculate scalpellomorphs, gave way to the low-profile, heavily armored sessile forms (DARWIN, 1854; NEWMAN *et al.*, 1969; NEWMAN & ROSS, 1976). This adaptation, sessility in addition to heavy armament, was evidently made initially in response to the same selective pressures that led to heavier armament and changes in shape in gastropod mollusks; namely, the rise of fish and invertebrates capable of crushing their prey (VERMEIJ, 1977; NEWMAN, 1979).

Although the spectacular radiation of the balanomorphs did not get underway until the Oligocene (NEWMAN & STANLEY, 1981), divergence of the sessile suborders was mostly completed by the Upper Cretaceous (NEWMAN *et al.*, 1969; Fig. 7 herein). This timeframe apparently coincided with greater volcanic activity and active sea-floor spreading in the western Pacific (HESSLER & LONSDALE, 1990; KERR, 1991), and on many South Pacific seamounts now represented by guyots in the Northwest Pacific (WINTERER *et al.*, 1993). Under such conditions, relatively local opportunities for entering the hydrothermal environment would have been greater than they were

throughout the Tertiary. Appropriate taxa diversifying and radiating at the time might be expected to have members that would become adapted to the relatively unexploited and abundant niches becoming available. However, reduction of hydrothermal activity and the concomitant loss of habitat leading to present conditions, and the warming of the deep sea at the end of the Paleocene considered deleterious to the normal inhabitants of the deep sea (KENNETT & STOTT, 1991), would likely have helped preserve the ancient character of the well established vent fauna by further deterring immigration of comparable modern forms.

It is understandable why, in light of this history and the current prevalence of a diverse Mesozoic vent barnacle fauna, few if any Cenozoic forms have been able to immigrate. Not only is the vent habitat, with its fluctuations in temperature, high sulfide content, and relatively low oxygen, a severe one to adapt to, but the general niches for barnacles are apparently already filled. Yet there were barnacles present in the Paleozoic; why are none of them represented? Earlier perturbations in the history of marine ecosystems may explain their absence, such as that culminating with the Permo-Triassic boundary. Furthermore, Paleozoic thoracicans were limited to pedunculate forms, and they were lightly armored compared to the Mesozoic scalpellomorphs (NEWMAN *et al.*, 1969; COLLINS & RUDKIN, 1981; SCHRAM, 1986). It is therefore likely that the advent of the same selective pressures that apparently led to heavy armament as well as the emergence of sessile forms in late Mesozoic, would have contributed to the extinction of most if not all Paleozoic forms wherever they occurred.

Contemporary hydrothermal vent barnacles have not fully escaped predation pressures for, while predators such as asteroids (TUNNICLIFFE, 1991; JOLLIVET *et al.*, 1989) and boring gastropod mollusks (MCLEAN, 1988) are absent, and fish capable of crushing shelled prey have yet to be observed (COHEN & HAEDRICH, 1983, COHEN *et al.*, 1990; GEISTDOERFER, 1991), galatheid and brachyuran crabs, and caridean shrimp, are commonly encountered (TUNNICLIFFE, 1991). The galatheids and carideans can pick with their chelipeds and, therefore, are likely capable of preying on freshly settled and young barnacles. On the other hand, true crabs are noted for their crushing abilities which, when it comes to barnacles, are more effectively applied to pedunculate than to sessile forms (NEWMAN, 1979, 1980, 1985). True crabs from vents are bythograeids and they appear capable of taking at least *Neolepas* if not the mature sessile barnacles.

The presence of such crustacean predators in the vent environment of the West Pacific could explain the absence of relatively unarmored Paleozoic barnacles. But perhaps more importantly, it may also explain the high ratio of sessile to pedunculate forms, which is the reverse of what is generally observed in the surrounding deep sea (NEWMAN & ROSS, 1971; SPIVEY, 1981) where predators such as true crabs are for some reason rare or absent (WILSON & HESSLER, 1987).

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Note added in proof

A highly relevant paper by VERMEIJ (1995)* appeared while the present paper was in press. It concerns the special physical conditions underlying the dramatic early Paleozoic and late Mesozoic episodes of biotic originations and radiations involving a rise in predation pressure and a concomitant rise in mineralized skeletons. The author attributes these two episodes to the spread of equable and productive epicontinental seas in response to an increase in submarine volcanism. This scenario not only relates well to the later Mesozoic origin and radiation of the sessile barnacles in shallow water, but to the adaptation of some to the more prevalent hydrothermal vent conditions of the time. VERMEIJ goes on to discuss how reductions in these resources, due to a decrease in submarine volcanism and the withdraw of epicontinental seas, lead to numerous biotic restrictions and/or extinctions. Such a reversal would be less severe where refugial conditions exist, and that provided by reduced but persistent bathy-abyssal hydrothermal activity in the western Pacific has been sufficient to perpetuate a likely reduced but still notable diversity of largely sessile late Mesozoic barnacles that otherwise went extinct.

* VERMEIJ, G. J., 1995. — Economics, volcanoes, and Phanerozoic revolutions. *Paleobiology*, **21** (2): 125-152.